

# AUSTRALIAN POPULATIONS OF THE *NACTUS PELAGICUS* COMPLEX (REPTILIA: GEKKONIDAE)

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An analysis of morphometric traits and scalation reveals that the Australian populations of the *Nactus pelagicus* complex differ from all other complex members by the presence of smooth subcaudal scales. This unique trait indicates that Australian *Nactus* represent a distinct clade from the New Guinea and Oceania populations. Other features of scalation (number of prelocaal pores, presence/absence of femoral pores) suggest that the northern and southern populations are distinct from one another. For these two groups, *Heteronota eboracensis* Macleay is available for the northern species and *Gymnodactylus cheverti* Boulenger for the southern one. □ *Reptilia, Squamata, Gekkonidae, Cape York Peninsula, geographic variation.*

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Two species of *Nactus* are known to occur in Australia. Both are confined to Cape York Peninsula (CYP). The recently discovered *Nactus galgajuga* is restricted to the boulder fields of the Trevathan Mtn Ra. (Ingram, 1978). In contrast, the second species is broadly distributed on the peninsula from the Cairns area to the Torres Strait Is (Fig. 1). Until recently, the widespread Australian *Nactus* was known as *N. pelagicus*; however, *pelagicus* is the proper name for the unisexual populations of *Nactus* occurring in Oceania (Zug & Moon, 1995).

The bisexual populations of Vanuatu, Solomon Is, New Guinea and its satellite island groups, and Australia have a number of available names. If these bisexual populations represented a single species, name assignment would be a simple matter of priority of publication. Moritz (1987), however, showed that several bisexual species exist. Among his six bisexual samples from Australia, Papua-New Guinea (PNG) and Vanuatu, he delineated three population-groups (Australia, PNG, Vanuatu) with different karyotypes and molecular traits. A preliminary morphometric and scalation survey across the entire range of *Nactus pelagicus* sensu lato indicated that several populations were morphologically distinct from one another and that at least three morphotypes occur in New Guinea (Moon & Zug, unpublished data). Zug & Moon (1995) compared the unisexual populations of Oceania to the adjacent bisexual populations of Vanuatu and the Solomon Is and showed that the bisexual populations were morphologically distinct and warrant recogni-

tion. The specific name *multicarinatus* Günther is available for this species.

The preliminary analysis also revealed that Australian populations were morphologically distinct from those of PNG. This observation was not unexpected, because Moritz (1987) had shown the Australian population to be karyotypically and biochemically distinct. Further, Greer (1989: 71) had suggested that two allopatric and morphologically distinct populations exist in Australia, a northern one separated from the southern 'in the vicinity of Princess Charlotte Bay'. Here, I offer an analysis of intra- and inter-population variation among CYP populations and confirm the existence of two species.

## MATERIALS AND METHODS

Specimens of *Nactus pelagicus* sensu lato were examined from throughout CYP, the Torres Strait Is, and adjacent Fly R. floodplain of PNG (Fig. 1). Most specimens were grouped into local samples representing discrete geographic areas, usually 30km or less in diameter. The major sample localities (n > 10 adults) are (N to S; also see Fig. 1 & Appendix: 1): PNGW, Fly R. delta, mainly in vicinity of Emeti; TORR, southern Torres Strait Is; SOMER, Somerset at tip of CYP and localities immediately to the S; MAPO, Mapoon; WEIPA, Weipa; IRON, Iron Ra.; WENL, Wenlock; MCIL, McIlwraith Ra.; COOKT, Cooktown; CHIL1, CHIL2, Chillagoe. Minor sample localities (n < 10) include (N to S): VRIL, Vrilya Pt; NOAL, N Alice R. crossing; HORSE, Horse Trailer W. H.; FLIN, Flinders I. group; NYMPH, Nymph I.; LAURA, Laura;

MTCAR1, MTCAR2, Mt Carbine; TINA, Tinaroo; DUNK1, DUNK2, Dunk 1.; and the TYPES, Endeavour R. and Fitzroy I. I also examined but did not record complete data for individuals from other Australian localities to ensure that these individuals match the characteristics of individuals in nearby samples.

The data set consists of 11 mensural and 18 scalation characters (Table 1). These characters represent a reduced data set from the set used in the study of the Oceania, Vanuatu and Solomons populations (Zug & Moon, 1995), with uninformative characters and ones with high recorder error (inconsistency) being deleted. Other characters have been modified or added. These are: MENSURAL – Eye Diameter (redefined), Interorbital Distance; MERISTIC – Femoral Pores, Femoral-Precloacal Pore Series Contact, Postmental-Infralabial Contact, Postmental Scale Size, Subcaudal Scales, Tubercle Density on Thigh. Eye diameter (EyeD) is the greatest horizontal distance across the exposed eyeball. Interorbital distance (Interorb) is the transverse distance between the anterior edges of the orbits. Femoral pores (FemPor) is the total number of femoral pores on the left and right thighs. For both femoral and precloacal pores, I recorded only the pores perforating their scales as shown by a secretion plug. Pore contact (PoreC) indicates whether the femoral and precloacal pores form a continuous series. Postmental-infralabial contact (PmLab) is the number of scale rows between the enlarged postmental and the infralabial scales and has several states: in contact, no scale rows separating postmental and infralabials (0); one scale row separating them (1); two scales rows separating them (2); etc. Postmental scale size (Postm) is the area of the right postmental, expressed as the number of chin scales occupying an equivalent area and is always expressed as an even integer. Subcaudal scales (Subcaud) is the presence (0) or absence of keels (1) on the scales of the ventral surface of the unregenerated tail. Tubercle density on thigh (TubDens) is the relative density of enlarged tubercles on the anterodorsal surface of the thigh and has three states: no or widely spaced small tubercles (0); a few widely spaced enlarged tubercles (1); many, often nearly abutting, enlarged tubercles (2). The abbreviated names in Zug & Moon (1995) for these characters have been expanded to improve recognition within the text; the original abbreviations are identified in Table 1.

The condition of bilaterally symmetrical characters on the right side (unless damaged) was recorded. Measurements were taken with dial

TABLE 1. Character set for members of the *Nactus pelagicus* complex. Previous characters are synonyms of the character names from Zug & Moon (1995). Definitions as in Zug & Moon, 1995: table 1. Modified (\*) and new characters are defined in the text.

Abbreviation	Character	Previous character
<b>Measurements</b>		
EyeD	Eye diameter	*ORD
HeadH	Head height	HH
HeadL	Head length	HL
HeadW	Head width	HW
Interorb	Interorbital distance	new
NarEye	Nares to orbit distance	NAOR
NeckL	Neck length	NL
SnForel	Snout to forelimb distance	SFL
SVL	Snout-vent length	SVL
SnW	Snout width	SW
TrunkL	Trunk or body length	BL
<b>Scalation</b>		
CloacS	Cloacal spurs	CS
CST	Cloacal spur's tip	CST
DorsTub	Rows of dorsal tubercles	DTR
FemPor	Femoral pores	new
ForefL	Forefoot lamellae	FFL
HindfL	Hindfoot lamellae	HFL
Inflab	Infralabial scales	IL
Palm	Palm scales	SCP
PmLab	Postmental-infralabial contact	new
PoreC	Femoral and precloacal pores continuous	new
Postm	Postmental scale size	new
PreciPor	Precloacal pores	PRCP
Subcaud	Subcaudal scales	new
Suplab	Supralabial scales	SL
TubRow	Tubercles in a parasagittal tubercle row	TR
TubHip	Tubercle rows over hips	DTH
TubHindl	Tubercle distribution on hindlimb	THL
TubDens	Tubercle density on thigh	new

calipers to the nearest 0.1 mm. Examination of the gonads revealed sex and maturity. Mature ♀♀ possess vitellogenic follicles >1.5 mm, oviducal eggs, or stretched oviducts; mature ♂♂ have enlarged testes and epididymides. The presence or absence of functional precloacal pores cannot be used to determine maturity because these pores are absent in adult ♂♂ of some Australian populations.

SYSTAT modules were used (DOS ver. 5.0 & Windows ver. 6.0.1) for the statistical analyses. Intrasample comparisons for identification of sexually dimorphic characteristics relied on the Bartlett's test for homogeneity of variance and the Student's t-test for equality of means. These same tests were used for examining the variation between samples and were complemented by



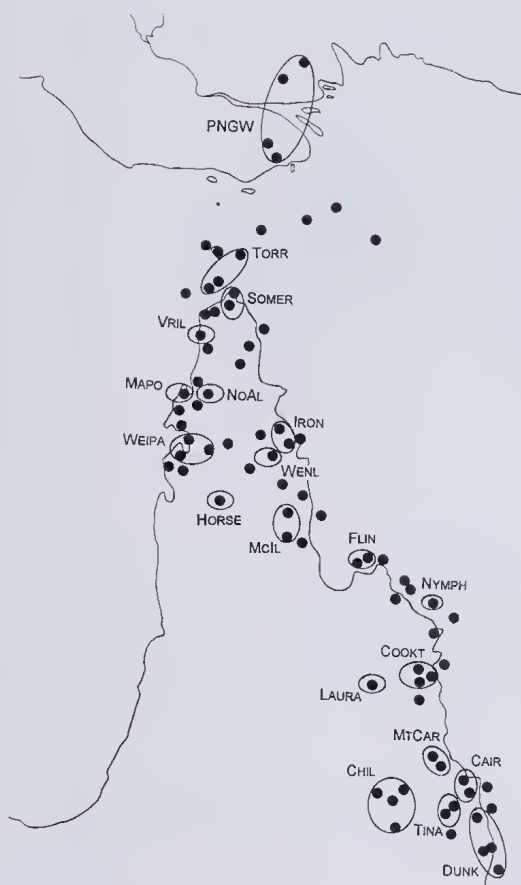


FIG. 1. Geographic occurrence of the *Nactus pelagicus* complex members in Australia and the location of sample localities for this study. ● = museum-vouchered specimen. Locality abbreviations explained in the text and in Appendix 1. Wellesley Is record (Bauer, 1994: map 40) is unconfirmed.

multivariate analyses. Principal Components Analysis (PCA) examines and estimates levels of phenetic similarities among the samples and potentially discerns patterns of geographic variation. The PCA covariance matrices derived from transformed (natural logarithms) for the mensural characters and raw data for scalation. Discriminate Function Analysis (DFA) assists in the identification of character(s) defining the a priori groups and possibly reveals mis-identified individuals. In the multivariate analyses, I used only specimens with complete data, and the mensural and meristic character sets were examined separately. Only seven localities had samples with sufficient adult geckos for a meaningful examination of sexual dimorphism: COOKT  $n = 16$  ♀♀,

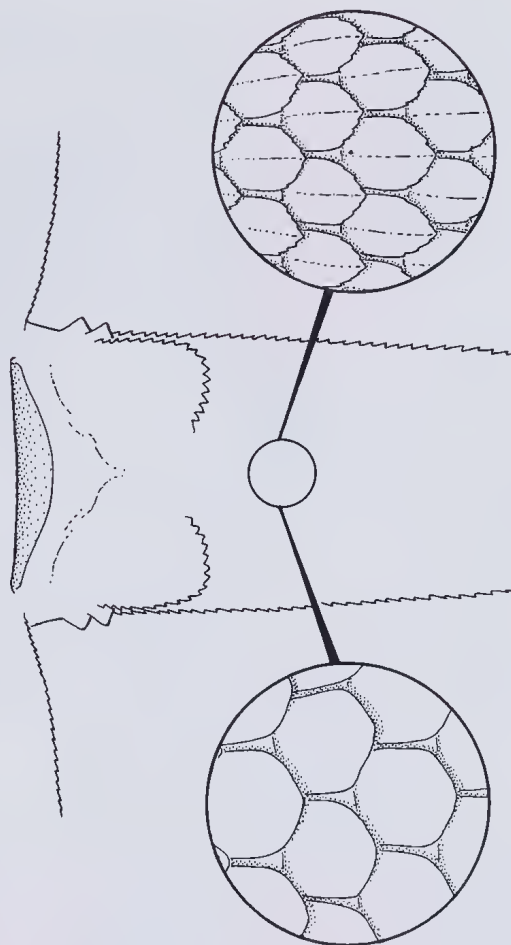


FIG. 2. Ventral view of the tail in *Nactus pelagicus* complex showing schematically two types of subcaudal scales, smooth (lower) and keeled (upper).

17 ♂♂; IRON  $n = 8, 12$ ; MCIL  $n = 5, 18$ ; PNGW  $n = 13, 11$ ; SOMER  $n = 11, 17$ ; TORR  $n = 13, 6$ ; WEIPA  $n = 16, 16$ .

Statistical comparison proceeded in a step-wise fashion: 1) to test for sexual dimorphism; 2) to determine the nature and level of intrapopulational variation and variation among neighbouring samples; 3) to search for regional patterns of concordant and/or discordant variation, to identify speciation of populations. Mensural traits were compared only among adults; all ages were used for comparison of meristic traits.

## RESULTS

**SCALATION. Sexual variation.** The presence of functional precloacal and/or femoral pores marks maturity in the ♂♂ of many gecko species, and

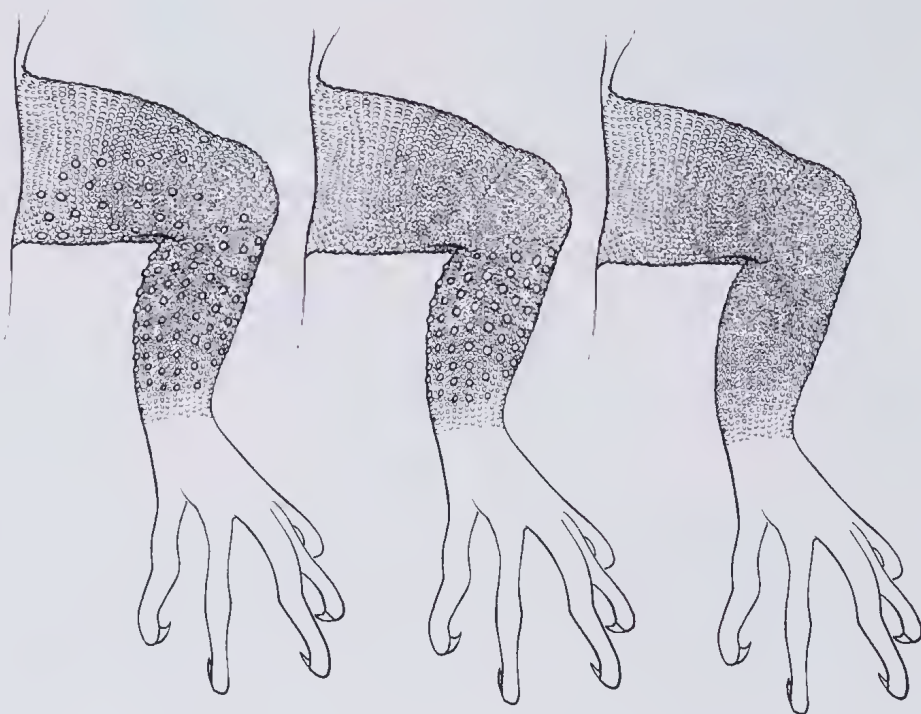


FIG. 3. Dorsal surface of the hindlimb depicting schematically the three states of hindlimb tuberculation: tuberculate (left), naked thigh (center), and atuberculate (right).

these pores are commonly absent in adult ♀♀. The pattern of occurrence in the Australian *Nactus* samples is variable for precloacal and femoral pores, and pores are not a reliable indicator of maturity. Functional precloacal pores occur in all mature PNGW, TORR, WEIPA, HORSE, MTCAR1, MTCAR2 and CAIR ♂♂. Active pores occur in some ♂♂ from the SOMER (88%), VRIL (50%), MAPO (30%), NOAL (75%), IRON (83%), WENL (50%), MCIL (94%), FLIND (40%), COOKT (47%), CHILI (33%) and DUNK1 (33%) samples. Mature ♂♂ from CHIL2 and TINA lack functional pores. In the northern sample (MCIL and northward), the number of active pores is typically six or more; whereas in the southern samples, ♂♂ seldom have more than three functional pores. Also an occasional adult ♀ in a few northern samples (TORR [AMSR44241], WENL [AMSR-105345]) possesses precloacal pores although usually fewer pores than ♂♂.

Femoral pores occur in some ♂♂ of the TORR (50%), SOMER (24%), NOAL (75%), WEIPA

(56%), IRON (33%), HORSE (100%) and MCIL (11%) samples, and in one specimen each of the ♀ TORR (AMSR44241) and WEIPA (AMSR82395) samples. All adult ♂♂ of the PNGW sample and of the Australian samples S of and including FLIND lack femoral pores. ♂♂ in the northern VRIL, MAPO and WENL samples lack femoral pores. When present, femoral pores lie distally on the thighs, seldom more than three or four on each side, and commonly bilaterally asymmetrical. Because femoral pores are absent or distally placed, PoreC is not used in the subsequent analyses.

In the six larger Australian samples, there are no significant sexual differences in scalation, aside from the presence or absence of pores, in the TORR and MCIL samples; only CST (mean = 0.50, 0.05; ♀♀, ♂♂) in SOMER, TubRow (mean = 25.1, 28.7) and Palm (mean = 5.8, 5.2) in WEIPA, TubDens (mean = 0.62, 0.08) in IRON, and Suplab (mean = 3.4, 3.1) in COOKT are significantly different ( $p < 0.05$ ) between the sexes. All characters, except CST, in these samples

TABLE 2. Summary of variation in the scale characters of the Australian *Nactus pelagicus* complex. n = sample size. See Table 1 for character abbreviations and Appendix 2 for a summary of scalation by sample locality.

	Suplab	Inflab	Postm	PnLab	DorsTub	TubRow	TubHip
n	273	273	272	272	273	272	272
Mean $\pm$ SD	3.3 $\pm$ 0.44	2.9 $\pm$ 0.50	13.4 $\pm$ 3.83	0.01 $\pm$ 0.12	14.2 $\pm$ 1.05	22.9 $\pm$ 4.96	8.0 $\pm$ 0.53
Range	3-4	2-4	2-26	0-1	11-18	15-37	4-12
Coef Var (%)	13.5	16.9	28.7	820	7.4	21.7	6.7
	TubHindI	TubDens	CloacS	CST	ForefL	HindfL	Palm
n	272	239	272	268	272	269	272
Mean $\pm$ SD	1.9 $\pm$ 0.33	0.2 $\pm$ 0.36	1.6 $\pm$ 0.52	0.1 $\pm$ 0.34	14.2 $\pm$ 1.02	18.2 $\pm$ 1.29	5.3 $\pm$ 0.86
Range	1-2	0-1	0-3	0-1	11-18	14-23	3-8
Coef Var (%)	17.7	238	32.8	258	7.2	7.1	16.2

display a homogeneity of variance between the sexes. The PNGW  $\delta\delta$  and  $\eta\eta$  are similar in all scalation characters.

Because most characters are not sexually dimorphic and the few showing dimorphism are unique to a specific locality, scalation, with the exception of the pore traits, is assumed to be sexually monomorphic in the Australian *Nactus pelagicus* complex. Subsequent geographic analysis of scalation includes individuals of all ages and sexes in each locality sample; pore number (FemPor, PreclPor) is excluded from some analyses.

**Geographic variation.** All Australian *Nactus* (including *N. galajuga*) possess smooth subcaudal scales (Fig. 2). Presently, all other known members of the *N. pelagicus* complex from New Guinea into Oceania possess keeled subcaudals. Keeled subcaudal scales, no or small postmental scales (Postm), and numerous (>30) tubercles in the dorsal tubercle rows (TubRow) differentiate the PNGW sample from all known populations of Australian *N. 'pelagicus'*. These differences suggest that PNGW represent a distinct species and is likely not a member of the Australian clade, so it is excluded from further comparisons.

The preceding sexual comparisons reveal that in all samples except CHIL2, TINA and DUNK2, some mature  $\delta\delta$  have precloacal pores. There appears to be a break between MCIL and FLIND with pores regularly >6 in northern populations and usually <3 in the southern ones. The occurrence of some  $\delta\delta$  with femoral pores shows a similar geographic break, with FLIND  $\delta\delta$  and all samples to the S lacking femoral pores and some  $\delta\delta$  in MCIL and other northern samples with femoral pores, although these pores are absent in the VRIL, MAPO and WENL samples. These three samples are small, and pores may be present in a few members of these populations but

were not found because the femoral pores usually occur in less than 50% of the  $\delta\delta$ .

Scale variation within the total Australian sample is summarised in Table 2 and the variation within and among the local samples in the Appendix 2. From the perspective of either the local samples or the total sample, Suplab, DorsTub, TubHip, ForefL and HindfL have low variability (cv < 15%) and show no geographic trends. Inflab, TubRow, TubHindI, and Palm are moderately variable (cv = 16-25%). Inflab, TubRow, and Palm generally show lower means in the S, but the pattern is not clinal. TubHindI shows two states in Australian *N. 'pelagicus'* (Fig. 3): tubercles on dorsal surface of both thigh and crus (tuberculate thigh); and tubercles on only the dorsal surface of the crus (naked thigh). Both states occur throughout CYP, although the naked-thigh state is absent in most samples N of and including COOKT, occurring at low frequency in the SOMER and FLIND samples and in the single NYMPH specimen. In contrast, from MTCAR southward, the naked-thigh state is common and the higher frequency suggested the segregation of the local samples into tuberculate- and naked-thigh samples (e.g., CHIL1, CHIL2, respectively).

The remaining characters range from borderline variable (Postm, CloaS) to extremely variable PnLab, TubDen, CST, PreclPor, FemPor). Postm shows the same variability in each local sample as in the total sample and suggests no geographic pattern. Throughout the Cape, most individuals typically have two cloacal spurs (CloaS) on each side of the tail base; however, the one-spur state has a higher frequency in northern samples. Cloacal spurs are more often rounded than pointed (CST), although the pointed state is common in MTCAR and TINA. The extension of chin scales between the postmental and the infralabial scales (PnLab) occurs in a single IRON specimen and in a third of the FLIND ones; in all other Australian specimens, the postmentals and



infralabials touch. Most Australian *N. 'pelagicus'* lack enlarged tubercles on the front of the thigh (TubDens) even if the thigh is tuberculate dorsally.

Even though there are no strong geographic patterns in scale variability, many neighbouring samples have one or more scale characters displaying significant differences ( $t < 0.05$ ), excluding comparisons with precloacal and femoral pores because of their dimorphism. The pair TORR-SOMER are significantly different in Postm, TubRow, ForefL and Palm. The pairs SOMER-VRIL and MAPO-VRIL have no differences, but MAPO-NOAL and WEIPA-NOAL differ in TubRow. MAPO-WEIPA differ in Suplab and HindfL. The E central samples display more significant differences between neighbouring sample pairs. WENL-IRON differ in DorsTub, ForefL, HindfL and Palm; WENL-MCIL by Inflab and TubRow; and MCIL-FLIN by Inflab, Postm, TubRow, TubDens, HindfL and Palm. The southern sample-pairs have low and moderate levels of differences. COOKT-MTCAR1 have no differences; COOKT-CAIR differ by Postm, TubRow and Palm; CHIL1-CHIL2 by TubRow, ForefL and Palm; and DUNK1-DUNK2 by TubRow. Within this southern area, the greater frequency of naked-thigh specimens warrants a comparison of the COOKT-LAURA-MTCAR1-CHIL1-DUNK1 sample (tuberculate) with the MTCAR2-CAIR-CHIL2-TINA-DUNK2 sample (naked). Seven characters show significant difference: Postm, DorsTub, TubRow, TubHindl, ForefL, HindfL and Palm (Table 3). The syntypic series of *marmorata* de Vis (= *cheverti* Boulenger) consists of naked-thigh specimens from Fitzroy I. and tuberculate-thigh ones from Endeavour R.; aside from the thigh tuberculation, the two sets of specimens differ only by TubRow and TubHindl. The large distance between COOKT and the E-central samples has a potential for major differences, yet COOKT-FLIN show only Palm differing, but COOKT-MCIL show Suplab, Inflab, Postm, TubRow, TubDens, CloaS and CST. Thus, COOKT-MCIL and MCIL-FLIN have a similar level of differences.

Although other paired comparisons are possible, the preceding ones explore the major regional

TABLE 3. Select mensural and scalation characters for southern naked-thigh (NYMPH, MTCAR2, CAIR, CHIL2, TINA, DUNK2) and southern tuberculate-thigh (COOKT, LAURA, MTCAR1, CHIL1, DUNK2) samples of *Nactus pelagicus*. Character name abbreviations as in Table 1.

Mensural Characters						
	SVL	TrunkL	HeadL	NarEye	Interorb	
Tuberculate (mean $\pm$ SD)	43.3 $\pm$ 2.6	17.9 $\pm$ 1.7	11.8 $\pm$ 0.6	3.7 $\pm$ 0.3	3.5 $\pm$ 0.3	
Range (n = 56)	38.4-50.0	14.4-22.3	10.6-13.5	3.1-4.3	2.8-4.2	
Naked (mean $\pm$ SD)	46.3 $\pm$ 4.1	20.0 $\pm$ 1.2	12.3 $\pm$ 1.2	3.9 $\pm$ 0.5	3.3 $\pm$ 0.3	
Range (n = 22)	39.2-57.0	13.2-25.4	10.4-15.6	3.1-5.2	2.8-4.2	
Scalation						
	Postm	DorsTub	TubRow	ForefL	HindfL	Palm
Tuberculate (mean $\pm$ SD)	15.8 $\pm$ 3.9	14.4 $\pm$ 1.1	18.0 $\pm$ 1.7	14.5 $\pm$ 0.9	18.3 $\pm$ 1.1	5.3 $\pm$ 0.9
Range (n = 69)	8-26	11-17	15-21	13-17	15-20	3-8
Naked (mean $\pm$ SD)	12.4 $\pm$ 4.0	13.6 $\pm$ 1.0	21.3 $\pm$ 3.2	13.5 $\pm$ 0.8	17.4 $\pm$ 1.4	4.9 $\pm$ 0.6
Range (n = 32)	2-24	12-16	17-27	12-15	14-20	4-6

ties, and additional ones appear redundant and do not demonstrate any additional variation patterns. Another approach is to examine the distribution of all individuals in multivariate space. Principal components analysis (all scale characters and all samples, including TYPE) examines the level of variation within all (or a select set of) scale characters of all sample localities simultaneously. PCA of the total character set (excluding only Subcaud which is invariant and TubDens which is not applicable to naked-thigh specimens) for the total Australian sample shows TubRow, Postm and PreclPor to have the major influence (PC loadings: -4.9, 1.8, -1.7, respectively) on the first factor or component. Postm and PreclPor are the major ones for the second component, and PreclPor for the third component. The first three components account for 87% of the total variance (50, 21, 16%, respectively). Bivariate scattergraphs of component pairs reveal no segregation of the samples in multivariate space. Similar results (Fig. 4) obtain with a PCA excluding the sexually dimorphic pore characters and TubDens. The sequence of component loading remains the same as in the total character analysis, except ForefL and HindfL replace the pore characters; the first three components account for 92% of the total variance. A varimax rotation of component axes yields some segregation of the northern and southern populations, although significant overlap occurs. The lectotype of *Heteronota marmorata* Macleay lies in the centre of the cluster.

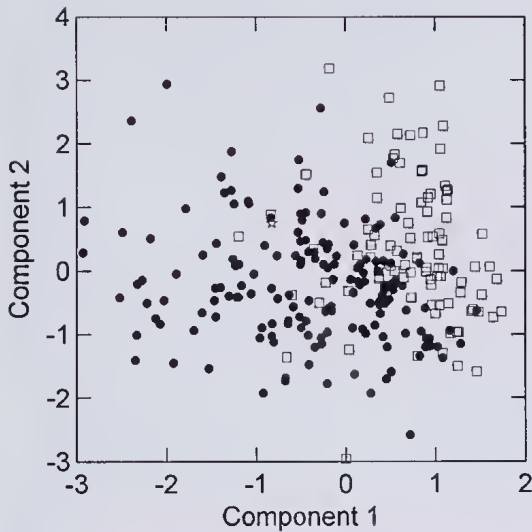


FIG. 4. Distribution of Australian *Nactus* in multivariate space derived from a PCA of scalation (covariance matrix, varimax rotation). The first component reflects mainly the variation of TubRow; the second component Postm and TubRow. ● = individuals of the northern population; □ = southern population; ☆ = lectotype of *Heteronota marmorata* Macleay (= *N. cheverti*).

Discriminant function analysis (DFA) permits a test of the uniqueness of a priori groups by identifying the character(s) that best segregate the groups and whether each individual is assigned to its a priori group. The subsequent DFA used 12 scalation characters, excluding the sexually dimorphic pore characters, TubDens (absent in naked-thigh specimens), PmLab (nearly invariant), and Subcaud (invariant), occasionally also excluding TubHindl.

DFA of naked- and tuberculate-thighs groups yields strong discrimination based mainly on TubHindl and assigns all naked-thigh individuals to their group and 98% of tuberculate-thigh group members to their group. The four individuals (2%; AMSR16479, 64046, QMJ26237, 36192) misclassified are the specimens with the naked thighs in the northern tuberculate-thigh samples. Reassigning these four individuals to the naked-thigh group and reanalyzing yields 100% correct assignment to both a priori groups; again TubHindl is the character weighed most strongly for discrimination classification.

DFA of the northern samples (TORR, SOMER, VRIL, MAPO, NOAL, WEIPA, HORSE, IRON, WENL, MCIL) and the southern ones (FLIND,

COOKT, MTCAR1 & 2, CAIR, CHIL1 & 2, TINA, DUNK), excluding TubHindl, yields moderate discrimination of northern and southern individuals, 85% and 82% correct a posteriori classification, respectively. The classification functions for each character differ little for the N and S groups and only Inflab, Postm and TubRow group-means (3.0, 2.7; 12.6, 14.8; 25.1, 19.1; respectively) differ by more than 0.3, and only Inflab and CloaS have moderately different weights for the classification functions. Misclassified northern individuals derive from six samples (TORR, SOMER, MAPO, WEIPA, IRON, MCIL) and southern ones from six samples (FLIN, COOKT, CAIR, CHIL2, DUNK2, TYPES [one each from Endeavour R. & Fitzroy I.]). With the exception of the entire CAIR sample ( $n = 5$ ), there is no obvious character or set of characters causing the misclassification. The combination of small Postm and high TubRow in the CAIR individuals appear to produce their incorrect group assignment.

DFA comparison of adjacent regional samples (same sample pairs as for the earlier  $t$  tests of scalation means) yields no northern samples in which correct classification is 100%. Among the southern samples, CAIR-COOKT, CHIL1-CHIL2, and DUNK1-DUNK2 have 100% correct group assignment, and this accuracy derives from TubHindl. Considering the possibility of three taxa (northern tuberculate-thigh, southern tuberculate-thigh, and southern naked-thigh [including the two insular naked-thighed individuals from FLIN and NYMPH]), DFA correctly classifies all southern naked-thighs, 94% of the southern tuberculate-thighs, and 85% of the northern sample. All misclassified southern tuberculate-thighs (4 of 66) are assigned to the northern sample. The misclassified northern specimens ( $n = 164$ ) are two to the southern naked-thighs and 23 to the southern tuberculate-thighs. TubHindl is the major discriminator, hence the misclassification of the two SOMER specimens with naked thighs. CST, Palm, and Postm are the next set of characters with the greatest differential weights.

**MORPHOMETRY. Sexual variation.** Among the six Australian samples (Table 4), TORR and WEIPA show no significant differences ( $p < 0.05$ ) between the meristic characters of ♀♀ and ♂♂. Variance is homogeneous between all samples for all characters. MCIL possesses significant differences between the sexes in only SVL, but variance is unequal between the two sexes. SOMER shows significant differences for only TrunkL and NeckL with ♀♀ having longer



TABLE 4. Select mensural parameters showing sexual dimorphism in some samples of adult Australian *Nactus*. Values are the mean  $\pm$  one standard deviation; character abbreviations as in Table 1.

Locality	♀ ♀				
	n	SVL	TrunkL	HeadW	NarOrb
TORR	13	47.8 $\pm$ 3.3	20.2 $\pm$ 1.8	8.7 $\pm$ 0.6	4.0 $\pm$ 0.4
SOMER	11	46.2 $\pm$ 3.8	19.9 $\pm$ 2.0	8.2 $\pm$ 0.9	3.8 $\pm$ 0.4
WEIPA	16	48.0 $\pm$ 3.4	20.5 $\pm$ 2.0	8.9 $\pm$ 0.5	4.2 $\pm$ 0.6
IRON	08	48.4 $\pm$ 3.5	20.1 $\pm$ 1.4	9.7 $\pm$ 1.0	4.1 $\pm$ 0.4
MCIL	08	49.8 $\pm$ 5.6	20.3 $\pm$ 3.2	8.9 $\pm$ 1.0	3.4 $\pm$ 0.4
COOKT	16	45.5 $\pm$ 2.5	18.6 $\pm$ 1.6	8.4 $\pm$ 0.5	3.4 $\pm$ 0.4
Locality	♂ ♂				
	n	SVL	TrunkL	HeadW	NarOrb
TORR	06	45.4 $\pm$ 3.3	18.8 $\pm$ 2.8	8.4 $\pm$ 0.7	3.8 $\pm$ 0.2
SOMER	17	44.7 $\pm$ 4.6	17.7 $\pm$ 2.1	8.2 $\pm$ 0.8	3.7 $\pm$ 0.4
WEIPA	16	47.1 $\pm$ 3.1	20.1 $\pm$ 1.7	8.5 $\pm$ 0.7	3.4 $\pm$ 0.4
IRON	12	44.8 $\pm$ 3.0	18.3 $\pm$ 1.1	8.1 $\pm$ 0.8	3.7 $\pm$ 0.4
MCIL	18	46.3 $\pm$ 2.0	19.0 $\pm$ 1.4	8.7 $\pm$ 0.7	3.6 $\pm$ 0.4
COOKT	17	42.1 $\pm$ 2.0	17.2 $\pm$ 1.5	7.9 $\pm$ 0.4	3.7 $\pm$ 0.3

trunks (mean = 19.6mm) and shorter necks (mean = 7.0mm) than ♂ ♂ (mean = 17.7, 7.6mm, respectively). IRON and COOKT possess similar suites of sexually dimorphic characters SVL, TrunkL, HeadL, HeadW, and Interorb; individually IRON also has ♀ ♀ and ♂ ♂ significantly different in HeadH and NarOrb and COOKT in EyeD. In both IRON and COOKT, ♀ ♀ (mean = 45.5, 48.5mm SVL) are larger than ♂ ♂ (mean = 42.1, 44.8mm SVL).

The New Guinea sample (PNGW) shows no significant differences between the mensural means of the ♀ ♀ and ♂ ♂. Variance is homogeneous between the sexes for all characters except NeckL ( $p = 0.03$ ). Because the PNGW sample lacks the unique subcaudal feature of all Australian *Nactus* and likely represent a different clade, it is excluded from further comparison.

IRON and COOKT have a similar suite of sexual dimorphic mensural traits, thus geographic variation among the Australian samples is examined only in adult specimens and separately by sex.

*Geographic variation.* The Australian samples show no pattern of size variation. Mean SVLs vary from 44.9 to 52.0mm in ♀ ♀ and from 40.4 to 48.6mm in ♂ ♂, although the larger samples ( $n > 5$ ) have narrower ranges of means (44.9-49.8mm ♀ ♀, 44.5-47.1mm ♂ ♂). The largest ♀ (57.0mm SVL) is from CAIR and the largest ♂ (57.6mm) is from SOMER. The small samples from many localities offer no confidence to either the presence or absence of any geographic size differences; however, the similarities of the mean SVLs among the larger samples and the low to moderate coefficients of variation ( $cv = 4$ -10%)

for all samples suggest a general size uniformity throughout the CYP populations. This uniformity is also indicated by moderate (7.5%) coefficients ( $cv$ ) for both the total ♀ (mean = 47.3  $\pm$  3.5mm,  $n = 111$ ) and the total ♂ (mean = 44.9  $\pm$  3.4mm,  $n = 132$ ) samples. This uniformity and consistency of means and standard deviations exist for all other mensural traits. Notably, the combined samples emphasize the presence of sexual dimorphism in all mensural traits ( $p < 0.02$ ), except NeckL ( $p = 0.20$ ).

Although the univariate comparisons of mensural traits reveal no regional differentiation, the tuberculate-thigh and naked-thigh

conditions suggest populational differentiation, and as in scalation, a MTCAR2-CAIR-CHIL2-TINA-DUNK2 sample represents the naked-thigh population. A comparison of this sample to a sample of all other sample localities shows only InterOrb differing in size (both ♀ ♀ and ♂ ♂) between the two combined samples. Multivariate analyses (PCA) of transformed variables, separately for adult ♀ ♀ and ♂ ♂, also demonstrates a size uniformity within each sex between the two samples. ♂ ♂ and ♀ ♀ share the same major variables (HeadL, SVL, HeadW) and the same loading ordering of these three variables on the first component; in both sexes, HeadL accounts for 53% of the total variance. These three variables account for 72.5% (♂ ♂) and 74.8% (♀ ♀) of the total variance. The first component is strongly size associated. No bivariate plot of any paired combination of the five components yields any striking outliers, and none of the nearby outliers consistently represents the same individuals. Type specimens were included in the analyses, and all, including the lectotype (AMSR42733) of *Heteronota marmorata*, lie within the PC centroids. Thus, no morphometric differentiation of naked- and tuberculate-thigh populations is evident.

## DISCUSSION

**LOCAL AND REGIONAL VARIATION IN CHARACTERS.** A striking feature of the Australian *Nactus* is the smooth subcaudal scales (Fig. 2). This feature is unique in Pacific *Nactus*, occurring only in *N. galgajuga* and the Australian *N. 'pelagicus'*. The Mascarene *N. coindemirensis* and *N. serpensinsula* also possess smooth



subcaudals. At this time, it cannot be determined whether this character state is primitive, shared-derived, or of multiple independent origins. Nevertheless, its occurrence does suggest a single ancestor for all Australian *Nactus*.

Greer (1989) suggested that adults from northern populations were larger than adults of southern ones (region of Princess Charlotte Bay being the dividing line). A preliminary analysis of small samples from both N and S of the bay confirmed this difference. The analyses here of major samples and the entire Australian sample, however, find no significant differences in mean body size between northern and southern samples, although the single major southern sample (COOKT) has the smallest mean SVL for both adult ♀♀ and ♂♂ (Table 4). In both northern and southern samples, ♀♀ regularly average larger than ♂♂, often significantly so, but these differences are not great, ranging 2-3mm. The other mensural characters show similar sexual dimorphisms that are statistically significant in the larger samples but slight in actual measurements and invisible to the human eye. None of the analyses of the mensural data reveals a pattern of regional differences and offers no evidence of genetic differentiation among the Australian populations. Because the differences are slight, are not evident in all mensural characters, and are not displayed in the same suites of characters in different samples, they are as likely to arise from measurement error and small sample sizes rather than being a reflection of microdifferentiation.

Greer (1989) also observed differences in the number of precloacal pores in the northern (5-11) and southern (0-3) populations. His observation holds with the addition of a qualifying statement: if pores are present in adult ♂♂. Precloacal pores do not occur in all adult Australian ♂♂; when present, northern ♂♂ have 4-11 and southern ones 1-5. With the exception of two northern samples (TORR, IRON), PrecIPor do not occur in adult ♀♀. The frequency of PrecIPor occurrence in ♂♂ is low in some northern samples (e.g., 30% MAPO) and can be strikingly different between adjacent sample localities (e.g., 30% MAPO vs 100% WIEPA, 83% IRON vs 50% WENL). Because only functional pores were recorded, their absence in some individuals may be due to individuals' larger than minimum adult size yet not sexually mature. Nonetheless, the absence of pores occurs in larger specimens as well as small ones. Another possibility is a cyclic nature to pore secretion, although one would as-

sume that nonperforated pores would be visible in the pore scales, but such a condition was not commonly observed. These observations and the erratic occurrence of femoral pores in ♂♂ with PrecIPor and even a few ♀♀ with PrecIPor suggest that precloacal pores are truly absent in some adult ♂♂. Only northern samples and not all of them have some ♂♂ with FemPor.

Scalation, aside from the precloacal/femoral pores, suggests no sexual dimorphism but shows high interpopulational variation, although quantitative differences among samples are slight. The most striking character difference is the presence or absence of tubercles (large keeled scales) on the thigh. Naked-thigh individuals are rare in the samples from the northern half of CYP, with only three specimens (2 SOMER & 1 FLIN) or approximately 1% of the total northern sample. In contrast, naked-thigh individuals comprise nearly half of the southern sample (NYMPH and southward). Although these morphs might represent two distinct populations in the S, no other aspect of scalation supports such an interpretation (see Appendix 2).

Scalation in general does not offer a strong argument for even the N-S segregation of populations. Often the variation between adjacent sample localities is as great or greater than between more distant ones. Visual inspection of the sample means for the samples (Appendix 2) suggests somewhat larger postmentals (Postm), higher number of dorsal tubercle rows (TubRow), more often one rather than two cloacal spurs (CloacS), and more palm scales (Palm), but the differences are weak and not consistent within either the northern or the southern sample.

Multivariate analyses also demonstrate weak differentiation among samples. PCA reveals no discrete clustering for any sample. It identifies Postm, TubRow, and PrecIPor as the major contributors to the variation among and within samples. DFA identifies TubHindI as the major discriminator for classifying a priori groups. When this character is removed, Inflab (infralabials), Postm, and TubRow become the major discriminators, but misclassification increases to 15-20% in contrast to the 0-5% when TubHindI is included in the analysis.

**SPECIATION.** The primary question is whether the observed morphological differentiation resulted from speciation of and within Australian *Nactus* 'pelagicus'. The uniqueness and uniformity of the subcaudal scales among Australian populations strongly indicates speciation.

Furthermore, Moritz's (1987) karyotype data of a single Australian population ( $2N = 38$ ) are strikingly different from any other '*pelagicus*' population ( $2N = 28, 35$  or  $36$ ). Donnellan & Moritz (1995) show that two Australian populations are more similar to one another in allozymes than to any New Guinean or Oceania populations. All these data support the recognition of the Australian populations as distinct species.

The second aspect of the question is whether speciation has occurred among the Australian populations. Although I am convinced that the regional differentiation reflects two, perhaps even three species, the nature of the morphological variation does not permit an unequivocal decision. I advocate the recognition of two species, a northern and a southern one, divided at the head of Princess Charlotte Bay as suggested by Greer (1989). The present samples cannot address whether these two species are allopatric, parapatric, or of limited sympatry. The number of precloacal pores and the presence or absence of femoral pores in adult ♂♂ are the only two characters that provide decisive evidence of distinctiveness. Inflab, Postm, CloacS, HindfL, and Palm show some tendencies to differ between the N and S groups, but the ranges of means of the N and S samples overlap and in each listed character, either a northern or a southern sample has a mean at the minimum or maximum of the other group's range.

The early recognition of naked-thigh individuals and their concentration in southern populations suggested to me that two species, naked-thigh and tuberculate-thigh, existed rather than the N-S speciation as proposed above. Perhaps the southern naked-thigh individuals do represent a separate species. While that concept is tempting, the available museum specimens suggest the co-occurrence of the two morphs, and I lack field experience with them to suggest that they are not microsympatric as well. Further, the low frequency occurrence of the naked-thigh condition in the northern samples negates the immediate recognition of the southern naked-thigh populations as distinct. Whether this trait differentiates species or represents a single genic polymorphism requires microhabitat observations and electrophoretic or DNA analysis.

Because of the equivocal nature of the northern and southern species, biogeographic comments are inappropriate. I note only that the two species' distributions match the CYP and Atheron areas of endemism found in other Australian plants and animals (Cracraft, 1991). Also the variation among neighbouring samples suggest that disper-



FIG. 5. Geographic distribution of *Nactus cheverti* (□) *Nactus eboracensis* (●), and *Nactus* sp-New Guinea (◇) in CYP and the Torres Strait Is; Δ = the restricted type-locality of *Heteronota marmorata* Macleay (= *N. cheverti*).

sal is low and that each population is experiencing and adapting to local selective pressures.

A noteworthy distributional feature is the occurrence of the New Guinean *Nactus* in the Torres Strait Is nearly to CYP (Fig. 5). They are potentially sympatric on only one island, Mount Ernest I. I have confirmed a single specimen of each species from this island. *N. eboracensis*' most northerly record is from Yam I., and the New Guinea *Nactus* occurs as far S as Hammond, Booby, Friday and Prince of Wales islands. No other lizard shows this distributional pattern, although *Gehyra baliola*, a New Guinean species, occurs in the NE Torres Strait islands (Darnley, Murray) and is replaced in the southern islands by *G. dubia* and an undescribed species (King et al., 1989).



## TAXONOMIC RÉSUMÉ AND CONCLUSIONS

Macleay (1878) was the first to recognize the distinctiveness of the Australian *Nactus*. Although his descriptions do not differentiate among the two Australian species of the *N. pelagicus* complex, he named specimens from Fitzroy I. and the Endeavour R. as *Heteronota marmorata* and two specimens from CY (presumably the telegraphic station or cape of that name at the tip of the peninsula) as *Heteronota eboracensis*. In his catalogue, Boulenger (1885) assigned *Heteronota marmorata* to the genus *Gymnodactylus*. His action made *marmorata* a secondary homonym and hence no longer available as a specific name for the Endeavour-Fitzroy populations; thus, he proposed the replacement name *cheverti* for *marmorata* Macleay. (I.C.Z.N. Article 59b – a junior secondary homonym replaced before 1961 is permanently invalid.) Boulenger (1885) also listed *eboracensis* as a *Heteronota*, noting his uncertainty of this assignment.

Macleay's and Boulenger's names remained unused until 1913 when F. Werner used *Gymnodactylus Cheverti* for a specimen he had acquired from Brisbane. Zietz (1920) referred to both *G. cheverti* and *H. eboracensis* for Fitzroy I. and northern Queensland specimens, respectively, in his catalogue of Australian lizards. The names again disappeared from the herpetological literature for over 60 years until Wells & Wellington (1984) resurrected *Nactus eboracensis* in their checklist, providing no analysis or explanation. Owing to the absence of justifications for their nomenclatural action, their usage was not adopted by the herpetological community.

None of the preceding usages or actions affects the availability of *Gymnodactylus cheverti* Boulenger and *Heteronota eboracensis* Macleay, hence these names can be assigned to the southern and northern species, respectively. The type locality of *H. marmorata* is precise and of unquestionable provenance, i.e., Endeavour R. and Fitzroy I., both of which are within the range of the southern species. Further, all syntypes are recognisably from the southern population and are so classified by discriminant function analysis. Kluge (1963) selected an adult syntype from Fitzroy I. as the lectotype, thus functionally restricting the type locality to this island. Under my two species interpretation, this lectotype selection has no effect on name assignment to the southern populations; however, if the naked-thigh *Nactus* is a separate species, then *cheverti* Boulenger becomes the name for the naked-thigh species and the southern tuberculate-thigh species has no available name.

The situation for the northern species is not as straightforward because the lectotype and paralectotype of *H. eboracensis* have deteriorated and are barely recognisable as specimens of *Nactus*. Thus, their condition excluded them from the character analyses. In addition, the type locality of *H. eboracensis* is given only as 'Cape York', which is insufficient to determine unequivocally whether the name applies to the entire Peninsula or the telegraphic station/cape at the tip of the Peninsula. I accept the latter interpretation, because Macleay used precise place names for his other taxa. Furthermore to ensure nomenclatural stability, I restrict the type locality of *Heteronota eboracensis* Macleay to the former telegraphic station of CYP (10°43'S 142°28'E).

In conclusion, the Australian species of the *Nactus pelagicus* complex are:

### *Nactus cheverti* (Boulenger)

*Heteronota* (sic) *marmorata* Macleay, 1878: 100. Type-locality, 'from Fitzroy Island and Endeavour River'. Kluge (1963) designated a lectotype (Macleay Museum R632, now AMSR42733), thereby restricting the type-locality to Fitzroy I. *Gymnodactylus cheverti* Boulenger, 1885: 41. Nomen novum for *Heteronota marmorata*.

**DEFINITION.** A bisexual *Nactus* ranging in adult size from 38.4–57.0mm SVL (♀, 41.6–57.0mm; ♂♂, 38.4–48.4mm). Head scales small and granular except for enlarged scales bordering nares and mouth; 3–4, usually 3, supralabials in front of orbit; mental scale pentagonal and extending posteriorly between pair of small to moderate-sized postmentals; postmental almost always in contact with first infralabial. Dorsally nape, neck, and trunk covered by small, multi-keeled, cone-shaped scales and longitudinal rows of large, multi-keeled, cone-shaped tubercles, 11–17, commonly 14–15, rows at midbody, 15–27 usually 20 or fewer, tubercles in the parasagittal row between the axilla and inguen, and 6–10, usually 8 rows across hips; ventrally small, flattened, uncarinate scales from throat to vent. Thigh and crus with moderate number of enlarged keeled tubercles among small cone-shape scales; thighs lack tubercles in 30–50% of individuals. Tail round in cross-section with moderate-sized, slightly overlapping, keeled scales dorsally; scales cycloid and smooth ventrally. When present, 1–5 usually 3 or fewer precloacal pores in adult ♂♂; no precloacal pores in adult ♀♀ and no femoral pores in ♂♂. ♀♀ and ♂♂ usually with 2, occasionally 1 or 3, cloacal spurs on each side of tail base. Subdigital lamellae

enlarged, undivided, and smooth; 12-17, usually 14 or fewer, lamellae on fourth finger, 14-20, usually 18, or fewer on fourth toe. Karyotype,  $2N = 35$  (Moritz, 1987).

DISTRIBUTION. Southern half of CYP from Flinders I. Group and Melville Peninsula southward.

### *Nactus eboracensis* (Macleay)

*Heteronota eboracensis* Macleay, 1878: 101. Type-locality, 'Cape York'. Kluge (1963) designated a lectotype (Macleay Muscum R975, now AMSR31940); the type-locality is restricted to CY (former telegraphic station) ( $10^{\circ}43'S$   $142^{\circ}28'E$ ).

DEFINITION. A bisexual *Nactus* ranging in adult size from 37.9-57.6mm SVL ( $\varnothing$ , 41.1-56.7 mm;  $\sigma$   $\sigma$ , 37.9-57. mm). Head scales small and granular except for enlarged scales bordering nares and mouth; 3-4, usually 3, supralabials in front of orbit; mental scale pentagonal and extending posteriorly between pair of small to moderate-sized postmentals; postmental almost always in contact with first infralabial. Dorsally nape, neck, and trunk covered by small, multikeeled, cone-shaped scales and longitudinal rows of large, multikeeled, cone-shaped tubercles, 12-18, commonly 13-14 rows at midbody, 15-37, usually more than 22, tubercles in the parasagittal row between the axilla and inguen, and 4-12, usually 8, rows across hips; ventrally small, flattened, uncarinate scales from throat to vent. Thigh and crus with moderate number of enlarged keeled tubercles among small cone-shape scales; thighs rarely lacking tubercles. Tail round in cross-section with moderate-sized, slightly overlapping, keeled scales dorsally; scales cycloid and smooth ventrally. When present, 4-11, usually 6 or more, precloacal pores in adult  $\sigma$   $\sigma$ ; occasionally 1-2 precloacal pores in adult  $\varnothing$   $\varnothing$ , and rarely 1-3 femoral pores in  $\sigma$   $\sigma$ , sometimes on one side only.  $\varnothing$   $\varnothing$  and  $\sigma$   $\sigma$  usually with 2, occasionally 3, cloacal spurs on each side of tail base. Subdigital lamellae enlarged, undivided, and smooth; 11-18, usually 15 or fewer, lamellae on fourth finger, 15-23, usually 18 or fewer, on fourth toe. Karyotype, unknown.

DISTRIBUTION. Torres Strait Is of Great Woody, Horn, Mount Ernest, Thursday, Wednesday, Yam, York, and the northern half of CYP from W side of Princess Charlotte Bay northward.

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## APPENDIX 1

**SPECIMENS EXAMINED.** The samples are divided into two sets. The first set includes the specimens used in the statistical analyses. The capitalised abbreviations of localities are used in the text; sample size in parentheses, sequentially adult ♀♀, adult ♂♂, juveniles. The second set contains specimens examined to confirm the specific identity of each individual. Both sets are ordered geographically N to S, E to W. Museum abbreviations follow Leviton et al., 1985.

**TYPES.**

- Heteronota eboracensis* Macleay: AMSR29951 (lectotype), 29952.
- Heteronota marmorata* Macleay = *Gymnodactylus cheverti* Boulenger: Endeavour R. AMSR31937-43; Fitzroy I. AMSR42733 (lectotype), 42734-35.
- PNGW southern Fly R. delta, Western Province, PNG, 8°05'S 142°50'-56'E (13, 11, 3) *Nactus* sp: MCZ123212 (Adiba); MCZ124299 (Boze); MCZ124313 (Mememorac); MCZ121165 (Wipim); MCZ131132-33, 141115, 141117-19, 141122-25, 141127-30 (Emeti); USNM195757, 325059-66 (Emeti).
- TORR Torres Strait Is, 10°15'-37'S 142°13'-28'E (13, 6, 1) *N. eboracensis*: MCZ124298, QMJ25658-59, 25695, 25821 (Hom I.); MCZ140953 (Mt Ernest I.); AMSR42241-42, 42379, 44241, 58959, MCZ137658-60, QMJ58151 (Thursday I.); AMSR61982, 61985 (Wednesday I.); QMJ52378, 52381, 52383 (Yam I.).
- SOMER tip of CYP, Somerset area, 10°50'-11°45'S 142°10'-35'E (11, 18, 0) *N. eboracensis*: AMSR16479, 38515-17, 38520, 38522, 56040, 56043, 56045-46, 56048, 56059, 56215, 56287, QMJ24670-71, 26237, 42785, 42789, 45587, 45589-90, 54018-19, 54023, 54029, 54034, 54037, 54102.
- VRIL Vrilya Pt, 11°13'S 142°07'E (1, 4, 0) *N. eboracensis*: AMSR99713-14, 99727, 99734, 99764.
- MAPO Mapoon Mission, 11°58'-59'S 141°53'E (8, 10, 0) *N. eboracensis*: AMSR99700-02, 99704, 99989-91, 105060, 105110, 105129-35, 105142, 126033.
- NOAL North Alice R. crossing, 12°04'S 142°21'E (2, 4, 1) *N. eboracensis*: AMSR99766, 99927, 99934-38.
- WEIPA Weipa, 12°44'S 141°52'E (16, 16, 0) *N. eboracensis*: AMSR22134, 22140-41, 62110, 62112-14, 62122, 62129, 82218, 82220-21, 82369, 82393-95, 82398-99, 105032-33, 105089-95, QMJ25768-69, 39767, 39789 39791.
- IRON Iron Ra. area, 12°37'-54'S 143°00'-24'E (8, 12, 3) *N. eboracensis*: AMSR38524, 38526, 69938-40, 81923, 94104-06, 94144, 94154-55, 94171, 94508, 94518, QMJ28043, 32010-12, 34377-79, 43649.
- WENL Wenlock R. crossing, 13°06'S 142°56'E (10, 2, 0) *N. eboracensis*: AMSR94021-24, 94026, 105345-50, QMJ26687.
- HORSE Horse Trailer W.H., 13°25'S 142°02'E (0, 1, 0) *N. eboracensis*: QMJ58211.
- MCIL Mcllwraith Ra., 12°43'-13°58'S 143°11'-32'E (5, 18, 0) *N. eboracensis*: AMSR16261, 16268-69, 16298, 16356, 16358, 16474, 16704-05, 16712, QMJ34466-68, 34526, 34537, 38103, 38105, 38143, 38308, 38460-61, 38464.
- FLIN Flinder I Group, 14°06'-13'S 144°15'-20'E (4, 4, 0) *N. cheverti*: QMJ36165, 36192, 36194, 36207-09, 36217-18.
- NYMPH Nymph I., 14°39'S 145°15'S (0, 1, 0) *N. cheverti*: AMSR64046.
- COOKT Cooktown area, 15°24'-28'S 145°06'-15'E (16, 17, 1) *N. cheverti*: AMSR26675, 26679, 26687, 26738-39, 31937, 31940, 31942, 69934-35, 69937, 85962, 85965, 126031-32, 126034-38, 126040, 126046-47, MCZ136021, 136023, 136028, 136030-31, 136155, 136161, 136166, QMJ25206, UMMZ131494-95.
- LAURA Laura, 15°40'S 144°31'E (1, 0, 0) *N. cheverti*: QMJ38009.
- MTCAR1 Mt Carbine area, 16°19'-41'S 145°01'-20'E (0, 6, 2) *N. cheverti*: AMSR63904-07, 63910-11, 63913 (Windsor Tableland); QMJ40640 (Mt Carbine).
- MTCAR2 Mt Carbine area, 16°19'-41'S 145°01'-20'E (1, 0, 1) *N. cheverti*: AMSR38506 (Mt Carbine); QMJ19332 (Mt Molloy).
- CAIR Cairns area, 16°55'S 145°46'E (2, 1, 2) *N. cheverti*: AMSR42734, 85949, 94523, 119680, MCZ118879.
- CHIL1 Chillagoe area, 17°09'-19'S 144°30'-145°13'E (0, 3, 3) *N. cheverti*: AMSR85961-65, QMJ47102.
- CHIL2 Chillagoe area, 16°19'S-17°53'S 144°30'-35'E (4, 3, 6) *N. cheverti*: AMSR85950-55, 86738, 86904, 142590, 14598, 143208, QMJ18038, 31234.
- TINA Tinaroo, 17°10'S 145°33'E (1, 2, 1) *N. cheverti*: AMSR85956-57, QMJ11801-02.
- DUNK1 Dunk I. & adjacent coast, 17°20'-57'S 146°01'-10'E (0, 2, 3) *N. cheverti*: AMR86734 (Bingil Bay); QMJ1908-09 (Dunk II.); QMJ30858 (Innisfall); QMJ55125 (Tully).
- DUNK2 Dunk I. & adjacent coast, 17°10'-50'S 145°15'-146°09'E (3, 1, 0) *N. cheverti*: AMSR 51534 (Russell I.); QMJ52982 (Watsonville); QMJ60832, 61112 (Hann's Tableland).
- UNKNOWN LOCALITIES CYP (1, 1, 0) *N. eboracensis*: MCZ 35135, UMMZ 35135.

Specimens examined to determine specific identity but not for statistical analyses.

*Nactus* sp New Guinea

TORRES STRAIT IS. Darnley: AMSR42624; Murray: AMSR4515, 42555, 42567-69, 42587-88, 44230, 44272, 45070, 45903-04, 45909-10, 45957-59, 46099, 46135-38, QMJ52384-89; Daur: AMSR45080-87; Badu (Mullgrave) AMSR58975-76, 59068, 59118; Moa (Banks): AMSR46694-95, 46697-706, 46794-97, 46886-89, 46891-95, 46897-900, 46968, 48584; Mount Ernest (Nagir, Nagheer): AMSR4516; Hammond: AMSR42268-69, 42309-15, 44243-44, 47050-58, 47354, 47356; Booby: AMSR36578, 49918, QMJ26003, 26005-007, 27360; Friday: AMSR38527-28, 48941, 48943, 48998-9000; Prince of Wales: AMSR46192-96, 46504-11, 46617-21, 48839-43, 48900-14, 55934-36, 59175, 59178, 59184.

*Nactus eboracensis* Macleay

TORRES STRAIT IS. Yam: AMSR42375, 42382, 423405-15, 61667, 61743-44, 61747-52, 61825-26, 61870-71, 62469, QMJ52380-83; York (Yorkc): AMSR44246-48, 44346-60, 44363-67; Wednesday: AMSR561968, 61981-85; Thursday: AMSR42241-43, 42322, 44241, 58959, QMJ52378-79; Horn: AMSR48426, 59149-52, 61885-86, 61888, 61918-24, QMJ25657, 25821; Great Woody: AMSR62010.

CAPE YORK. AMSR16261, 16268-69, 16298, 16337, 16339, 16356, 16358, 16474, 16479, 16704-05, 36822, 38507, 38512, 38515-17, 38520, 38522, 38524, 51558, 62117, 62120-21, 62133, 62135, 62137, 86946, 105186, 105314, 38508, 38513-14, 38518, 51559-60, 56746, 62111, 62116, 62118, 62123-24, 62128, 62132, 62136, 62138, 62199-200, QMJ23461, 23479, 23498-99, 23517-18, 24619, 24646, 24650-51, 24670-71, 25657-59, 25695, 25767-69, 25775, 25821, 26223, 26237, 26687, 27155, 28043, 28048, 32010-12, 23257, 34378-79, 34466-68, 34528-29, 34531, 34762, 35377, 34530, 34536, 38099-100, 38102, 38104, 38172, 38276-77, 38199-200, 38280, 38307, 38309, 38314, 38350, 38407, 38409, 38461, 38463, 39753, 39762, 39791, 42789, 43649, 43659, 45586, 45588, 54018-19, 54023, 54029, 54034, 54037, 54084, 54102, 57750, 57799-801, 58151, 58523, 58631-32, 58633.

*Nactus cheverti* Boulenger

CAPE YORK. AMSR26675-76, 26679, 26683, 26685, 26687, 26732-35, 26738-42, 37203, 38506, 51509-10, 51516-17, 51520, 51526, 51531, 51534, 63908-09, 63914, 64046, 64052, 85949, 85960, 86733, 86735, QMJ11140, 17524-25, 17805, 17819, 25205-06, 25290-91, 25309, 27138, 27257, 36165, 36202-203, 36207, 26209, 30858, 31713, 36192-94, 36217, 36755-56, 45933, 47593, 48087, 51122-25, 53124, 53126, 53137, 53147, 53154.

*Nactus galgajuga* Ingram

BLACK MTN. QMJ29474 (holotype), AMSR70110 (paratype), (non-types QMJ52973, 61070-72, 61095-96).

## APPENDIX 2

Summary of the mean values for the scale characters of the Australian samples of the *Nactus pelagicus* complex. Sample abbreviations are defined in Appendix 1 and character abbreviations in Table 1 and the Materials & Methods section.

	n	Suplab	Inflab	Postm	Dors-Tub	Tub-Row	Tub-Hip	Tub-Hindl	Tub-Dens	CloacS	CST	Precl-Por	Fem-Por	Forefl	Hindfl	Palm
TORR	20	3.3	3.1	12.1	14.0	22.8	8.2	2.0	0.0	1.4	.05	2.0	0.0	13.8	17.4	5.0
SOMER	28	3.2	2.9	14.3	14.1	26.1	8.0	2.0	0.1	1.7	0.2	4.0	0.0	14.3	17.0	5.7
VRIL	04	3.8	2.0	13.0	14.0	28.5	8.0	2.0	0.0	1.0	0.0	0.2	0.0	14.2	17.5	5.5
MAPO	18	3.4	3.1	13.3	13.8	25.2	7.9	2.0	0.1	1.7	0.1	1.3	0.0	14.1	17.0	5.6
NOAL	07	3.3	3.1	12.6	14.0	32.0	7.9	2.0	0.0	1.3	0.0	3.5	1.7	14.0	18.3	5.1
WEIPA	32	3.1	3.0	11.4	14.1	26.9	7.9	2.0	0.1	1.5	0.0	3.7	1.3	14.5	18.8	5.5
IRON	23	3.1	2.8	11.9	15.0	24.2	8.3	2.0	0.3	1.8	0.1	3.8	0.7	14.0	18.1	5.0
WENL	12	3.3	3.0	12.2	13.8	26.7	8.0	2.0	0.0	1.5	0.0	0.0	0.0	14.0	19.4	5.7
HORSE	01	4.0	3.0	10.0	13.0	30.0	8.0	2.0	0.0	2.0	0.0	5.0	0.0	14.0	18.0	7.0
MCIL	23	3.6	3.4	12.8	14.1	21.1	7.7	2.0	0.5	1.4	0.0	4.7	0.3	14.0	19.2	5.7
FLIN	09	3.4	2.0	15.6	14.0	17.3	7.8	1.0	0.1	1.8	0.0	0.2	0.0	14.0	18.1	4.0
NYMPH	01	3.0	2.0	14.1	15.0	19.0	8.0	1.0	-	2.0	0.0	-	0.0	15.0	17.0	5.0
COOKT	34	3.2	2.0	17.0	14.4	17.6	7.9	2.0	0.1	1.8	0.3	0.5	0.0	14.7	18.6	5.7
LAURA	01	4.0	4.0	14.0	14.0	19.0	8.0	2.0	0.0	2.0	0.0	0.0	0.0	14.0	19.0	4.0
MICARI	08	3.1	2.9	14.5	14.6	18.6	8.3	2.0	0.2	1.5	0.5	1.0	0.0	14.4	17.5	5.1
MICAR2	02	3.0	3.0	13.0	13.0	18.6	8.0	1.0	-	2.0	0.5	0.0	0.0	13.5	17.0	5.0
CAIR	05	3.2	2.0	08.4	13.8	25.6	8.0	1.0	-	1.0	0.0	1.0	0.0	14.0	18.4	4.4
CHIL1	06	3.0	2.5	13.3	14.2	17.8	8.0	2.0	0.3	1.5	0.2	0.2	0.0	14.0	18.0	5.3
CHIL2	12	3.2	2.7	12.6	13.7	20.2	8.0	1.0	-	1.7	0.2	0.0	0.0	14.2	17.4	4.5
TINA	04	3.0	2.8	14.5	13.8	18.5	8.0	1.0	-	2.0	0.5	0.0	0.0	12.5	16.0	4.8
DUNK1	05	3.0	2.4	15.2	15.2	20.0	8.0	2.0	0.2	2.0	0.0	0.4	0.0	13.8	17.0	4.4
DUNK2	04	3.2	2.8	14.5	13.2	23.8	8.0	1.0	-	2.0	0.0	0.0	0.0	14.0	17.5	5.2